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Spongivory on Caribbean reefs releases corals from competition with sponges

Abstract Competition for space is an important process on tropical coral reefs. Few studies have examined the role sponges play in community structure despite the fact that many sponges are competitively superior to reef-building corals in space acquisition. Surveys conducted throughout the Florida Keys indicated that *Chondrilla nucula* was involved in about 30% of all coral-sponge interactions; this sponge has also been observed in 40–50% of coral-sponge interactions on other Caribbean reefs. *C. nucula* is also the top prey item of the Hawksbill turtle, and among the preferred prey of several spongivorous fish. I examined how predation influenced sponge competitive abilities (particularly those of *C. nucula*), and whether this type of indirect effect had important consequences for community dynamics in the Florida Keys. Exclusion of sponge predators (primarily angelfish) resulted in increased sponge overgrowth, with a subsequent greater loss of coral cover, compared to uncaged pairwise interactions. When caged, the corals *Dichocoenia stokesii* and *Siderastrea sideraea* lost significantly greater surface area and number of polyps to the sponge *C. nucula* compared to uncaged interactions. For caged interactions involving the sponge *Ectyoplasia ferox*, there was a trend for greater loss of *S. sideraea* surface area and polyps compared to uncaged interactions. Predation had a greater affect on *C. nucula* than on any of the other sponges examined. Predator exclusion experiments performed with naturally occurring coral-sponge interactions demonstrated a significant decrease in total coral cover compared to uncaged controls. It is proposed that indirect effects arising from spongivory (especially consumption of *C. nucula*) may have large community consequences. Species diversity on Caribbean reefs may be maintained, at least in part, by spongivores.

Key words Indirect effects · Competition · Predation · Sponges · Caribbean coral reefs

Introduction

Determining the extent of species interdependency has long been a major goal of ecologists. It has been clear at least since Paine (1966) that indirect effects can have a large effect on community composition (see also early works cited in Jackson 1981). Nonetheless, studies designed to specifically examine indirect interactions have not been as common as those to study direct interactions, and many indirect effects have been discovered only after examination of unexpected results (Schoener 1993; Wootton 1994a). Given that indirect effects exert considerable influence on community structure in many systems (e.g., Paine 1969; Brown and Heske 1990), identifying and examining their influence on community composition is essential for understanding community dynamics (Strauss 1991; Schoener 1993; Wootton 1994a, b; Menge 1995).

Tropical coral reef communities are typically dominated by scleractinian corals, and early ecological work focused on identifying a competitive hierarchy for these species based on pairwise interactions (reviewed in Lang and Chornesky 1990). A number of studies also examined direct interactions involving interference competition between a wide diversity of sessile invertebrates (e.g., Rützler 1970; Jackson and Buss 1975; Glynn 1976; Vicente 1978, 1990; Suchanek and Green 1981; Wellington and Trench 1985). Despite this focus on direct, pairwise interactions, it has often been suggested that intense predation pressure on organisms that compete with corals may result in important community-wide

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indirect effects (e.g., Randall 1961; Suchanek et al. 1983; Glynn 1990; Pennings 1996). For instance, algae are common members of most coral reefs, and represent an important group of space competitors. Many species of algae outcompete corals for space, but their effect on coral populations is mediated by severe grazing pressure from urchins and fish (Sammarco et al. 1974; Sammarco 1982; Hay 1984; Lewis 1986; Hughes 1989, 1994; Coyer et al. 1993). Thus, coral reef community diversity and structure appear to rely heavily on the strong indirect effects of grazers. The fact that algal cover increased at the expense of coral cover after the die-off of a major grazer, the urchin *Diadema antillarum*, highlights the importance of indirect effects in reef community structure (Lessios et al. 1984; Hughes et al. 1987; Carpenter 1988; Hughes 1994). It is important to note that overfishing of scarids and acanthurids has been identified as a reason for the continued replacement of coral with algal populations (e.g., Hay 1984; Hughes et al. 1987).

Sponges are another conspicuous taxonomic group present on tropical reefs, yet little is known of their role in community structure. Sponges can equal or exceed the biomass, abundance, and diversity of corals on some Caribbean reefs (Reiswig 1971; Rützler 1978). In addition, corals and sponges commonly compete for space on many reefs, with up to 12 interactions per square meter, and studies have indicated that sponges are the superior competitor in 80% of these encounters (Vicente 1978, 1990; Suchanek et al. 1983). In one notable case, Bryan (1973) documented extensive takeover of a section of reef in Guam by an encrusting *Terpios* sponge (see also Plucer-Rosario 1987).

In spite of the abundance and competitive dominance of sponges, consistently high coral cover on Caribbean reefs indicates that sponges are somehow prevented from reaching their competitive potential. As with algae, one reason may be that sponges are extensively preyed upon (Feddern 1968; Randall and Hartman 1968; Meylan 1988; Hourigan et al. 1989; Wulff 1994; Pawlik 1997). Bakus (1964, 1966) demonstrated the ability of fish to restrict sponges to the undersides of coral slabs. Sponge predators are common on coral reefs, but little is known of their contribution to community dynamics. For example, the sponge *Chondrilla nucula* is one of the most aggressive competitors for space, yet is the top prey item in the diet of *Eretmochelys imbricata* (the Hawksbill turtle; Meylan 1988), and ranks second in occurrence in the diets of spongivorous fish (Randall and Hartman 1968).

Recent work by Pawlik and colleagues (Chanas and Pawlik 1995; Pawlik et al. 1995; Pawlik 1997, 1998; Swearingen and Pawlik 1998) has indicated that predation on sponges may have important community-wide implications. Indeed, it appears that at least eight species of sponge commonly found in mangrove and grassbed habitats are restricted to these environments by predators (Pawlik 1998). Pawlik (1997) has argued that the most palatable sponges will be restricted by spongivores to refugia within the reef or to mangrove habitats

(see also Bakus 1966). After these sponges have disappeared or become rare, spongivores preferentially consume fast-growing palatable species that can quickly replace lost tissue (Pawlik 1997). *C. nucula* may fit this description (Swearingen and Pawlik 1998). Pawlik's (1997) hypothesis provides a point of departure for studies of the community effects of spongivory. For instance, if fast-growing/palatable sponges were abundant on the reef because of the actions of spongivores (Pawlik 1997), then coral populations would face continual competition from these aggressive space competitors.

In this paper, I examine the effects of spongivory on competition for space between corals and sponges. Specifically, I ask whether spongivores reduce the rate that sponges can overgrow coral competitors. I was interested in determining whether interactions among corals, sponges, and spongivores result in an interaction chain type of indirect effect (sensu Wootton 1993) that helps maintain high coral coverage.

Materials and methods

Surveys

To assess the frequency of competitive interactions between sponges and corals in the Florida Keys, USA, I conducted surveys on nine reefs ranging from Key West to Key Largo. At each surveyed reef, 1-m-wide transects were run along a depth gradient (Schmahl 1990). The total area surveyed and depths of transects for each reef are shown in Table 1. For each transect, I counted the number of coral-sponge interactions, and recorded which species were involved in interactions. Survey data were used to rank the coral and sponge species most commonly involved in competitive interactions. Predator distribution and density were estimated during the surveys by counting angelfish observed while swimming along the transect. This method is valid because each of the five species of angelfish encountered (*Pomacanthus paru*, *P. arcuatus*, *Holacanthus ciliaris*, *H. bermudensis*, and *H. tricolor*) are highly conspicuous due to bright coloration, distinctive patterns, and cruising behavior. In addition, *P. paru*, *P. arcuatus*, and *H. tricolor* form territories which reduced the probability of double-counting.

Table 1 Survey data for nine areas throughout the Florida Keys. The depth of each survey, and total area surveyed (number of transects in parentheses) are shown. The average number of competitive interactions ($\pm$SE) between sponges and corals, and average predator density ($\pm$SE) were measured. Any coral and sponge that were in physical contact were considered to be interacting. Predator (i.e., angelfish) density was estimated by counting all fish observed while swimming along a transect

Reef	Depth (m)	Area surveyed (m^2)	Interactions (m^{-2})	Predator density (m^{-2})
Alligator	18	175 ($n = 9$)	0.39 (0.12)	0.24 (0.05)
Tennessee	18	340 ($n = 17$)	0.37 (0.06)	0.35 (0.05)
	9	120 ($n = 6$)	0.21 (0.08)	0.21 (0.03)
Turtle Shoals	3	75 ($n = 4$)	0.56 (0.32)	0.11 (0.02)
Western Sambo	12	47 ($n = 3$)	0.11 (0.08)	0.06 (0.04)
Sand Key	12	76 ($n = 4$)	0.20 (0.07)	0.17 (0.01)
Molasses	7–12	190 ($n = 10$)	0.23 (0.11)	0.32 (0.04)
Mosquito	1–2	175 ($n = 9$)	0.52 (0.20)	0.19 (0.04)
Florida Bay	1	500 ($n = 25$)	0.06 (0.02)	0

Caging experiments

To assess the effects of predator removal on coral-sponge interactions, I conducted caging experiments on Tennessee reef (24°45′N 80°45′W). The first set of experiments involved initiating pairwise encounters between two species of coral and three species of sponge in the presence and absence of angelfish predation. The second set of experiments involved caging naturally occurring interactions and comparing these to uncaged interactions.

For the first set of caging experiments, I initiated pairwise interactions between the corals *Dichocoenia stokesii* and *Siderastrea sideraea*, and the sponges *Anthosigmella varians*, *C. nucula*, and *Ectyoplasia ferox* at a depth of 8 m over an area > 300 m^2. This area was frequented by a pair of gray angelfish (*P. arcuatus*), at least two queen angelfish (*H. ciliaris*) and a French angelfish (*P. paru*). A Hawksbill turtle (*E. imbricata*) was also observed swimming over the site. The two gray angelfish may have included this site in their large territory. Each of these vertebrate species has a specialized diet that consists primarily of sponge (Randall and Hartman 1968; Meylan 1988; Hourigan et al. 1989; Wulff 1994).

The choice of coral species for these experiments was based on several factors. First, and most important, both corals are small (approximately fist size) and could be collected without injury (which might affect competitive ability). Second, they were locally abundant, and collections had little effect on local population densities. Finally, *D. stokesii* is an aggressive coral, thus providing a conservative test of the importance of indirect effects arising from predation. I chose the three sponge species because they are common members of most Caribbean reefs (e.g., Alcolado 1990; Alvarez et al. 1990; Diaz et al. 1990), and were often observed in competitive encounters with corals. Both *A. varians* and *C. nucula* have been shown to be superior space competitors to corals (Vicente 1978, 1990). I observed both *D. stokesii* and *S. sideraea* competing with all three sponges in the field. In addition, these sponge species are represented in the diets of angelfish and the Hawksbill turtle (Randall and Hartman 1968; Meylan 1988; Hourigan et al. 1989).

Ceramic tiles (15 cm × 15 cm) served as platforms for competitive interactions; corals were cemented to the tiles with epoxy putty (Z-spar), and sponges were attached using monofilament. Great care was taken to ensure minimal handling of corals and sponges after collection. I initiated interactions by orienting corals and sponges so that a zone of contact was established along the growing edge of both species (no other contact between coral and sponge was allowed). I mapped points of contact at the beginning of the experiment. Plastic mesh with large openings (≈ 25 cm^2) was used to construct cages, and these enclosures were placed over half of the interacting pairs ($n = 11$). It was not possible to use control cages in these experiments due to the small size of enclosures and large sizes of angelfish. Therefore, I determined whether cages had any effect on water flow by measuring rates of dissolution of plaster of paris clods (Wellington 1982). Clods were molded in plastic egg containers and attached to $8 \times 8 \times 0.5$ cm Plexiglass plates with rubber cement. I attached 36 clods to the wooden planks with cable ties; half were placed under cages, half were left exposed. After 2 days, I collected all clods and dried them for 48 h at 60 °C. Average clod weight loss under cages was compared with weight loss of exposed clods using Student's two-tailed *t*-statistic (Zar 1984).

Although light levels were not measured, enclosures had wide openings to allow maximal light penetration, and periodic cleanings prevented any algal buildup. Any reduction in light levels, however, would have affected the sponges *C. nucula* and *A. varians* as much as, or more than, the corals since both species harbor photosynthetic symbionts. Hill (1996) demonstrated that growth rates of *A. varians* were dependent in part upon healthy zooxanthellar symbiont populations, and *C. nucula* is reported to be a phototrophic Caribbean sponge (Wilkinson 1987a; Corredor et al. 1988). Thus, the competitive ability of both sponges would be diminished if cages reduced light levels significantly (providing a more conservative test for indirect effects).

Sponge growth was monitored for 10 months for all *S. sideraea* interactions and 12 months for all *D. stokesii* interactions. Fouling algae were periodically cleaned from enclosures, and 2 months was the longest interval between cleanings. If there was no interaction between corals and sponges at the termination of the experiment, I reattached those individuals at the site of collection. I measured overgrowth in two ways. I first measured the greatest distance that the sponge had grown over living coral perpendicular to the edge of the coral. I then estimated the area of living coral tissue that was lost using the "aluminum foil" method of Marsh (1970). All sponge tissue was removed from the coral skeleton at the end of the experiment to determine whether coral tissue was still present. After measuring surface area, I counted the number of polyps destroyed by the sponge to assess the effect of overgrowth on coral reproductive potential. Partially destroyed polyps were included in my counts since these polyps would be unlikely to contribute to gonad production. Statistical comparisons for all other interactions were made using Student's one-tailed *t*-statistic (Zar 1984).

To determine the community consequences of predator removal within a given area of reef, I conducted a second set of caging experiments. Seventeen interactions between sponges and corals were caged at 8 m depth. Another 8 interactions were included as uncaged controls. At the start of the experiment, small stainless steel nails were placed along the point of contact in each pairwise interaction to mark the initial line of encounter between species. I monitored this experiment for 18 months. The corals included *Acropora cervicornis* ($n = 1$), *D. stokesii* ($n = 5$), *Diploria strigosa* ($n = 2$), *Montastrea annularis* ($n = 4$), *M. cavernosa* ($n = 4$) and *S. siderea* ($n = 9$). The sponges included *Amphimedon compressa* ($n = 2$), *Anthosigmella varians* ($n = 5$), *Callyspongia vaginalis* ($n = 4$), *C. nucula* ($n = 9$), *Cliona caribbea* ($n = 1$), *Ircinia felix* ($n = 2$), and *Niphates erecta* ($n = 2$). I observed French, gray, blue and queen angelfish as well as a Hawksbill turtle at this site. Lateral overgrowth was measured from the original point of contact (i.e., the nail) perpendicularly to the edge of new sponge growth. Surface area lost to and polyps destroyed by sponge overgrowth were not measured. I compared lateral overgrowth between caged and uncaged replicates using Student's one-tailed *t*-statistic (Zar 1984).

Results

Surveys

On average, I observed fewer than one coral-sponge interaction per square meter in the Florida Keys (Table 1). The most common sponges and corals that were observed competing for space are listed in Table 2. *C. nucula* was involved in almost twice as many competitive encounters as the second sponge on the list (i.e., *Mycale laevis*). *M. laevis* is typically found on the undersides of corals, and it is not clear whether this association is competitive or mutualistic (Goreau and Hartman 1966). I considered interactions involving *M. laevis* to be competitive based on several observations of overgrowth by this sponge in the field. *C. nucula* interacted with a wide diversity of corals (nine species), and it should be noted that this sponge is not abundant on Florida reefs (e.g., Schmahl 1990). Thus, it is involved in more interactions than would be predicted based solely on its abundance. *S. siderea*, on the other hand, was the most commonly observed coral in general surveys of community structure (i.e., surveys other than those to estimate the frequency of competitive encounters); therefore, the frequency of interactions observed for this coral appears to match its relative abundance.

Table 2 List of sponges and corals most frequently observed in competitive interactions on Florida reefs. Values are compiled from surveys done at Alligator, Molasses, Tennessee, Western Sambo, and Sand Key reefs. A total of 282 coral-sponge interactions were recorded

| Sponge	Frequency	Coral	Frequency
Chondrilla nucula	0.29	*Siderastrea siderea*	0.39
Mycale laevis	0.15	*Agaricia* spp.	0.14
Anthosigmella varians	0.11	*Porites astreoides*	0.11
Amphimedon compressa	0.08	*Montastrea cavernosa*	0.10
Ircinia felix	0.07	*M. faveolata*	0.08
Ectyoplasia ferox	0.06	*Diploria strigosa*	0.06
Ulosa ruetzleri	0.06	*D. labarynthiformis*	0.03
Xestospongia muta	0.06	*M. franksii*	0.02

Angelfish were not observed in the Florida Bay but inter-island pilings and bridge supports were typically occupied by juveniles and some adults. Predator density was typically higher at depths greater than 8 m (Table 1). Predator density was higher in the Upper (Molasses and Mosquito reefs) and Middle (Alligator and Tennessee reefs) Keys than in the Lower Keys (Western Sambo and Sand Key reefs). *H. tricolor* was the numerically dominant angelfish on reefs below 8 m (data not shown).

Caging experiments

The number of replicates in the experimental manipulation experiments was reduced by cage and/or specimen loss. *E. ferox* was especially prone to dislodgement, and six *D. stokesii* died from unknown causes (i.e., they showed signs of pigment loss). Analysis of clod card dissolution rates (g day^{-1}) revealed no differences in water motion between treatments [caged and uncaged means ($\pm$SD) were 5.31 (1.20) and 5.67 (0.95), respectively; $n = 18$ for both treatments, $P > 0.3$].

Interactions between both species of coral and *A. varians* were unaffected by the presence of predators (Fig. 1). *D. stokesii* appeared to be competitively superior to *A. varians* since there was a clear zone of inhibition between interacting pairs ($\approx$1 cm); sponges also suffered loss of zooxanthellae and showed evidence of damaged tissue. This phenomenon was not observed in the other coral-sponge interactions. I could not measure surface area, and therefore polyp loss, for interactions involving *A. varians* since overgrowth was minimal or non-existent.

Predation had the greatest effect on the overgrowth capabilities of *C. nucula*; growth of this sponge over both corals was greater in the absence of predation (Fig. 1, Table 3). I observed numerous bite marks on exposed individuals whereas no evidence of predation was present in the caged replicates. There was a significant increase in lateral overgrowth in the absence of predators in the *E. ferox–S. sideraea* interactions (Fig. 1). In addition, there was a strong trend for increased loss of surface area in these pairwise interactions in the absence of predators (Table 3). Predator removal reduced the amount of overgrowth for *E. ferox–D. stokesii* interactions by approximately 30% (Fig. 1, Table 3), but there was little power to detect significant
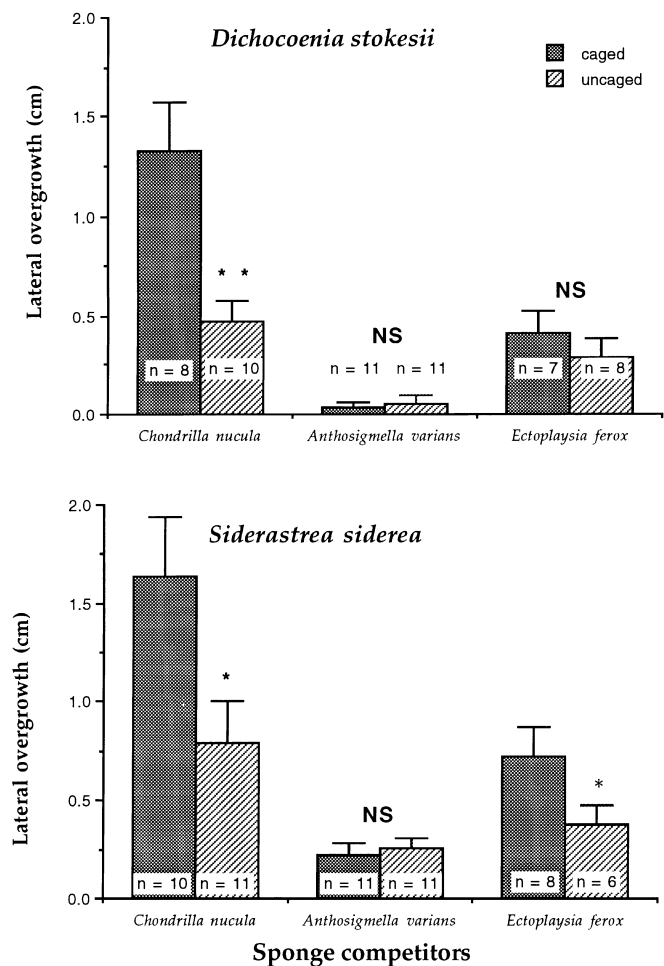
Fig. 1 Effect of predator removal on lateral distance of sponge overgrowth. Sponge growth was measured perpendicular from the edge of the coral to the greatest distance covered by the sponge. Sample sizes are shown within each bar. *Error bars* indicate +1 SE (*$P < 0.05$; **$P < 0.01$; *NS* not significant)

differences. For interactions involving *E. ferox*, bite marks were apparent on uncaged but not caged individuals.

D. stokesii has larger, more widely spaced polyps than *S. sideraea*, thus in general fewer polyps were lost per unit surface area. There was a greater total loss of reproductive units (i.e., polyps) for replicates protected from predation compared to replicates exposed to predation for interactions involving *C. nucula* (Table 3). For the *D. stokesii–C. nucula* interactions, two replicates

Table 3 Effects of predator removal on coral tissue lost to, and polyps destroyed by sponge overgrowth. Tissue loss was calculated as the amount of surface area covered by new sponge growth. Values represent means ($\pm$SE), and sample sizes are as shown (*C* caged, *U* uncaged, *D. s. Dichocoenia stokesii*, *S. s. Siderastrea siderea*, *C. n. Chondrilla nucula*, *E. f. Ectyoplasia ferox*)

Interactions	Treatment	n	Coral tissue lost (cm^2)	P	Polyps lost	P
D. s. × *C. n.*	C	8	5.54 (1.25)	< 0.05	6.38 (1.36)	< 0.05
	U	10	2.28 (0.52)		3.10 (0.81)	
D. s. × *E. f.*	C	7	1.09 (0.26)	NS	1.43 (0.43)	NS
	U	8	0.72 (0.24)		1.50 (0.53)	
S. s. × *C. n.*	C	10	7.17 (1.05)	< 0.05	31.9 (5.51)	< 0.05
	U	11	3.88 (0.85)		17.7 (3.94)	
S. s. × *E. f.*	C	8	1.75 (0.34)	< 0.06	8.75 (2.00)	< 0.07
	U	6	0.97 (0.25)		4.67 (1.12)	

protected from predation lost $>25\%$ of their total polyps. One caged replicate in the *S. sideraea–C. nucula* interactions lost $>40\%$ of its total polyps. There was no significant difference in the number of *D. stokesii* polyps destroyed by *E. ferox* in either caged or uncaged treatments. For *S. sideraea–E. ferox* interactions, however, there was a marginally non-significant trend for greater loss of polyps in caged replicates (Table 3).

During the 18 months that I monitored experiments with naturally occurring interactions on Tennessee reef, five cages were lost, and two *D. stokesii* and one *S. siderea* died after pigment loss. In the absence of predation, lateral overgrowth of sponges increased by over 100% compared to uncaged controls. Mean ($\pm$SE) values were 1.95 (0.35) and 0.72 (0.47) for caged ($n = 11$) and uncaged ($n = 6$) treatments, and this difference was significant ($P < 0.05$).

In these experiments, *C. nucula* was represented to a greater degree than any other sponge (36% of all sponge competitors). Two replicates involved interactions between *A. varians* and *D. stokesii* and in neither case did the sponge show any signs of tissue damage resulting from coral aggressiveness as was observed in the experimental manipulations. Predation was observed on sponges involved in interactions exposed to predation, while no signs of predation (e.g., bite marks) were observed on sponges in enclosures.

Discussion

Coral reefs of the Florida Keys appear to have far fewer competitive interactions per square meter than reefs elsewhere in the Caribbean. For example, while on average less than one interaction per square meter was observed in this study (Table 1), Suchanek et al. (1983) found approximately six interactions per square meter between 8 and 18 m depth in St. Croix, USVI, and Vicente (1990) found up to ten interactions per square meter in Puerto Rico. One reason for the discrepancy between this study and the others is that I included only corals and sponges in my surveys whereas several taxa (such as gorgonians) were included in the other surveys. However, sponges represented $>80\%$ of the interactions in many of the surveys in Suchanek et al. (1983). A more reasonable explanation may be that overgrowths were infrequent because coral cover is relatively low, and bare space is relatively common, on Florida reefs. Interaction chains involving spongivores (and hence indirect effects) may not be as important on Florida reefs as they would be in areas with relatively higher coral cover and greater species diversity. Furthermore, sponge growth rates and competitive abilities may be greater on Caribbean reefs than reefs in the Pacific due to higher productivity in the former (Wilkinson and Cheshire 1990). If so, indirect effects arising from spongivory may be of greater ecological importance in the Caribbean. To determine the generality of findings reported here, it is necessary to examine the effects of spongivory on reefs with greater coral cover and in areas with less productivity.

The results of experiments in this study, however, clearly demonstrate the existence of an interaction chain type of indirect effect involving corals, sponges, and spongivores. As with other studies in marine environments (Menge 1997), indirect effects were detected in a relatively short amount of time. In the experiments reported here, predator presence reduced the rate of coral surface area lost to sponge overgrowth by approximately 50% (range 34–58%; Table 3). Any magnitude of change in abundance caused by indirect effects that is greater than 10% is considered to be ecologically significant (Menge 1995).

In the absence of spongivory, it appears that *C. nucula* would soon overgrow the majority of corals with which it interacts, since none of the corals examined to date can deal with the rapid growth rates and aggressiveness of this sponge (Fig. 1, Table 3; see also Vicente 1990). This is particularly important given that approximately 30% of all coral-sponge interactions involved *C. nucula* in the Florida Keys (Table 2). On Mosquito Banks, for example, *C. nucula* was abundant and involved in $>70\%$ of all overgrowths (Table 1). Elsewhere in the Caribbean, *C. nucula* has been shown to be involved in nearly half of all scleractinian coral competitive interactions (Suchanek et al. 1983; Vicente 1990), and can occupy up to 12% of available space (Corredor et al. 1988). These observations highlight the potential effect *C. nucula* could have on reef structure if this sponge were not the top prey item in the diet of several spongivores (Randall and Hartman 1968; Meylan 1988).

Experiments involving *E. ferox* were ambiguous (Fig. 1, Table 3). Although there was a trend for greater overgrowth in the absence of predation, further work is necessary before any general conclusions can be drawn for this species. However, *E. ferox* appears to be chemically defended (Pawlik et al. 1995), and this may explain the slow rates of overgrowth observed in this study. Defense and (re-)growth may represent alternative strategies for sponges dealing with grazing/predation, as has been proposed for plant populations dealing with herbivores (van der Meijden et al. 1988; Herms and Mattson 1992).

The inability of *A. varians* to overgrow *D. stokesii* and *S. siderea* in the pairwise experiments was unexpected (Fig. 1). Many interactions involving these species were observed during surveys, and the sponge rarely showed any deleterious effects due to the coral. In addition, sponge overgrowth was observed in the two replicates involving *D. stokesii* and *A. varians* that were caged in experiments involving naturally occurring interactions. However, in some overgrowth interactions involving *Montastrea* spp. in the wild, the leading edge of *A. varians* appeared bleached (i.e., white due to the loss of zooxanthellar symbionts), but necrosis has not been observed. One explanation for the observed bleaching and necrosis is that *A. varians* requires a period of acclimation before overgrowth can proceed. The conclusion that *D. stokesii* was a better competitor than *A. varians* is suspect since field observations indicate the opposite.

Two general observations can be made at this point. First, it seems that the indirect effects observed in this study may have important evolutionary consequences given that spongivores increase the reproductive potential of corals by reducing their loss of polyps to sponge overgrowth (Table 3). The role that indirect effects play in the evolution of interacting species has been neglected, but may be of great importance (e.g., Miller and Travis 1996). Indirect effects arising from spongivory may influence the evolution of coral competitive abilities because, by removing the effects of competitors, spongivores effectively remove selective forces that might encourage production of aggressive characteristics. Thus, coral aggressiveness may correlate with the level of protection afforded by consumption of potential competitors. Second, a major problem facing coral reefs today is offshore sewage outflow from onshore development (see Maragos et al. 1985). Given that there is a positive correlation between sponge growth rates and eutrophication (Wilkinson 1987b, c; Wilkinson and Cheshire 1990), coral populations may be further jeopardized by increases in nutrient levels. Zea (1994) found that both sponges and algae outcompeted corals in eutrophic regions, but sponges outcompeted algae when turbidity was high (as would be expected when phytoplankton populations increase due to elevated nutrient levels; Birkeland 1987). Continued eutrophication, therefore, will favor sponge populations at the expense of both coral and algae.

Further work on the importance of short-chain indirect effects on coral reef community dynamics is necessary. Spongivores clearly influence coral-sponge interactions and thus play a role, which may be underestimated, in community function. As with algae, sponges appear to be restricted in their dominance of the reef by the actions of specialist consumers. Compared to herbivorous fish, however, spongivores are not as numerically abundant. Angelfish and the Hawksbill turtle, therefore, may represent a true keystone guild (sensu Power et al. 1996) in that their effect on community structure might be greater than their numbers suggest. If spongivores represent keystone species, then conservation biologists should consider the effects that widespread angelfish harvesting is having on reef communities. Several fish collectors operate out of Key West, but John Pennecamp State Park located in Key Largo (i.e., Upper Keys) does not allow fish harvesting. The decline in angelfish density towards the Lower Florida Keys (Table 1) may reflect increased harvesting activities on those islands. It is unknown what effect reduction of Hawksbill turtle populations by harvesting has had on reef structure (Meylan 1988), but given that these turtles spend 92% of daylight hours foraging (van Dam and Diez 1997), loss of this predator has probably had a major impact on reef populations. Overfishing has been identified as a major cause of coral reef degradation (Hay 1984; Hughes 1994), and the effect of spongivore removal on Caribbean reefs should be examined more fully.

Some of the most abundant sponges on Caribbean reefs (i.e., encrusting sponges) are also the most aggressive competitors for space (e.g., Suchanek et al. 1983; Corredor et al. 1988; Alcolado 1990; Alvarez et al. 1990, Diaz et al. 1990; Schmahl 1990). It is important to note that these sponges are commonly the top prey items in spongivore diets (e.g., *C. nucula* Randall and Hartman 1968; Meylan 1988). Spongivores have been shown to affect species richness by excluding from the reef sponges that typically live in mangrove environments (e.g., Dunlap and Pawlik 1996; Pawlik 1998). This study also suggests that spongivores play a major role through indirect effects in the persistence of currently observed patterns of species diversity in many coral reef communities.

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